LONG TERM CHANGES IN INTERTIDAL ZONATION IN TASMANIA WITH SPECIAL REFERENCE TO THE MOLLUSCA

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(Plates 2-3; text fig. 1.)

Abstract.

A study carried out over eleven years of the intertidal zonation in Tasmania shows certain changes which take place over a long period of time. These changes affect many groups of organisms, but the most serious effect is upon the Mollusca, so that lists of molluscan species of an area can vary greatly from year to year. Interspecific competition is important in long term changes.

Introduction.

The usual method of studying the intertidal zonation is for several visits to be made to one area over a short period of time and the results then written up. In many cases the area is then abandoned completely or else visited sporadically. The present paper is based upon the results of regular visits to four localities over a period of eleven years. On each visit the shore was examined in some detail and major changes in zonation were noted. Each locality was visited once per annum at approximately the same time of the year, and some places were visited more frequently. Certain algae which are known to fluctuate seasonally in density on the shore are not included in this study. These are *Ulva lactuca* (L.), *Colpomenia sinuosa* (Roth.) Derby & Sol. and *Scytosiphon lomentarius* (Lyng.) Ag.

The ecological nomenclature used is that of Stephenson & Stephenson (1949), and the author of each species is only cited once.

It is essential to state that the phenomena recorded below have been noted on shores of a low tidal amplitude, about 2′ annual average tides with a maximum of 5′ at springs. Further, all the localities concerned suffer moderate to low wave action. The latter type of coast was selected because the fauna of coasts suffering intense wave action is liable to be severely altered by gales. Although such changes may be widespread, it is other longer period changes which are the subject of the present study.

Specific Examples of Changes.

The four localities at which regular visits were made are Dodge's Ferry, Coles Bay, Fisher Island and Blackman's Bay (text fig. 1). The results obtained at these places have been confirmed by examinations of the shore at other localities.

(1) *Dodge's Ferry.*

Dodge's Ferry is situated on a sheltered coast in southern Tasmania. One of the features of the shore in December, 1949, was the very well developed belt formed by the serpulid worm, *Galeolaria caespitosa* (Lam.). This species, of encrusting habit, formed a massive belt up to 5″ in thickness on the rocks. The spaces below and around the worm tubes

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Text Fig. 1.

were inhabited by a numerous fauna consisting of *Kellia australis* (Lam.), *Mytilus planulatus* (Lam.), *Austromytilus rostratus* (Dunker), *Lepsithais vinosa* (Lam.), *L. reticulata* (Blain.), *Sypharochiton maugeanus* Iredale & May, polynoid, phyllodocid and nereid worms and the anemone *Actinia tenebrosa* (Farq.). The molluscs may be considered as characteristic of the fauna to be expected on this part of the shore.

During the year 1950 the tube masses broke away from the rock, and instead of the thick belt of *Galeolaria* there remained only a thin scattered layer of tubes. Since 1950, there has been a slow colonization of the shore by *Galeolaria* with the result that the tubes now form a more or less continuous sheet on the rocks at the appropriate tidal level. However, there is not yet any development of the thick masses of worm tubes. Living amongst the *Galeolaria* tubes in March, 1958, and utilizing the rock as a substratum was a numerous fauna consisting of *Cominella lineolata* (Lam.), the buccinids *Lepsithais reticulata* (Blainville) and *L. vinosa,* the chitons *Poneroplax albida* (Blainville) and *Sypharochiton maugeanus* Iredale & May, the limpets *Patelloida alticostata* and *Chiazacmea flammea* (Quoy & Gaim.), the siphonarians *S. diemenensis, S. funiculata* and *S. tasmanica,* the nassariid *Tavaniotha tasmanica* (Ten.-Woods) and the thaid *Agnewia tritoniformis.*

Certain of these species are not usually associated with *Galeolaria* masses. *Poneroplax albida* generally is considered an inhabitant of the Infralittoral fringe, but is sometimes found at higher shore levels. The feeding habit of this chiton, together with its large size, prevents it from living amongst the fully developed *Galeolaria* masses. The limpets, *P. alticostata* and *C. flammea*, as well as the three species of *Siphonaria* and *Tavaniotha tasmanica* also are not usually found in the *Galeolaria* belt.

In addition to the appearance of the above species, *Kellia australis* had disappeared from the tidal levels at which it was previously found. This lamellibranch requires small spaces in which to live, and this environment is usually supplied by *Galeolaria* tubes, seaweed holdfasts or by the coralline alga *Lithophyllum hyperellum* (Foslie).

In 1949, the *Galeolaria* masses were replaced at lower tidal levels by beds of *Mytilus planulatus* (Lam.), which in turn were replaced by the ascidian *Pyura stolonifera* (Heller). In 1956 the mussel beds were almost non-existant, the mussels being confined to the lower part of the *Galeolaria* belt, which extended as far as the *Pyura* belt (Plates 2 and 3). The *Pyura* belt had extended up the shore to meet *Galeolaria*, and the belt was more densely populated by ascidians.

The removal of the mussels was not caused by a gale, since the region where the beds were found is in a sheltered locality where strong enough seas for this purpose could not arise. The cause of the disappearance is not known. However, the effect upon the fauna is very great. The mussels, which were packed closely together, furnished a sheltered habitat for many species. The most common of these were *Cominella lineolata, Patelloida alticostata, Notoacmea corrosa* Oliver, *Venerupis diemenensis* Q. & G., *Kellia australis* (in byssus strands), *Ostrea virescens* Angas, *Hiatella australis* (Lam.), the crabs *Helice haswellianus* Whitelegge, *Petrolisthes elongatus* M. Edwards, *Halicarcinus ovatus* (Stimpson), numerous worms, amphipods and isopods, as well as algae such as *Ulva lactuca* L. *Polysiphonia* spp., *Laurencia botryoides* (Gaill.) and *Gigartina* sp. The barnacles *Chamaesipho columna* (Spengler) and *Chthamalus antennatus* (Darwin) lived attached to the shells of the mussels.

Consequent upon the disappearance of the mussels, the great majority of this fauna disappeared from the appropriate shore level. The only species still to be found were *Patelloida alticostata, Helice haswellianus,* and the two species of barnacles together with a few *Mytilus planulatus,* which remained either as isolated individuals or as scattered small clusters.

The recolonization of a denuded area by *Mytilus* usually starts soon after the clearing of the rocks. It was noticed at Blackman's Bay that rocks which were covered by *Mytilus* beds were very rapidly recolonized by mussels after they had been denuded by a storm (Guiler, 1954). The same process started less rapidly at Dodge's Ferry, but it has now reached a stage where mussels are common on the rocks.

The upward spread of the ascidian *Pyura stolonifera* (Heller) has already been noted. This species furnishes a habitat which is suited to some species of mollusc, notably *Acanthochiton sueurii* (Blainville), *Sypharochiton maugeanus, Amaurochiton glaucus* (Gray), *Patelloida alticostata* (Angas), *Cominella lineolata, Kellia australis, Venerupis exotica* (Lam.), *Dentimitrella lincolnensis* (Reeve), *Dicathais orbita* (Gmelin). Other species found are the echinoderms *Heliocidaris erythrogramma* (Val.), *Uniophora sinusoidea* (Perrier), *Coscinasterias calamaria* and *Tosia aurata* (Gray), the crustaceans *Halicarcinus ovatus* (Stimpson), *Petrolisthes elongatus,* and the sponges *Hymeniacidon perlevis* (Montagu) and *Tethya diploderma* (Schmidt).

(2) *Coles Bay.*

I have already drawn attention to the change in zonation at Coles Bay (Guiler, 1953). It was found in 1950 that *Mytilus planulatus* and the alga *Hormosira banksii* (Turn.) Decaisne were in very intense inter-specific competition. In 1956, it was found that *Hormosira* has become more numerous and was dominant over the mussels, particularly at localities known as Honeymoon Beaches. The same situation is true at the present time. However, at the Fisheries, both in 1956 and 1958, the reverse held true, *Mytilus* having achieved dominance. These results suggest that there may be frequent changes in dominance between these two species in this area.

The *Galeolaria* belt, which was very well developed in 1950 and virtually absent in 1953, has not yet regained a place of ecological importance on the shore.

The belt formed by *Austromytilus rostratus*, but poorly developed in 1950, had extended by 1953, and by 1958 was a very prominent feature of the shore. This mussel does not have as many species associated with it as *Mytilus*, and being a smaller mussel, does not offer such an extensive habitat between the mussels and the substratum.

(3) *Fisher Island.*

This island is situated near the southern end of Flinders Island in Bass Strait, and is the site of a small Biological Station. The island was first visited in March, 1954, and subsequently in November, 1956, and February and March, 1957. During this period the most significant change has been the development of a *Hormosira* belt in the Midlittoral at the southern end of the island. In 1954, *Hormosira* was linked with *Galeolaria* as forming a joint belt on the eastern shore of the island, but since then it has spread to such an extent that it forms a band all around the island at the bottom of the *Galeolaria* belt. Correlated with the appearance of the *Hormosira*, there is an apparent lessening in the width of the *Galeolaria* belt. However, the tubes of *Galeolaria* still exist, and are occupied by worms, on the rocks among the *Hormosira* plants. There is no evidence that in recent years *Galeolaria* has formed a thick incrustation on the shores of Fisher Island, though there was a thick incrustation on sheltered parts of the island in 1957 (Guiler, Serventy and Willis, 1958). However, the typical fauna of the *Galeolaria* belt was poorly developed.

Modiolus pulex Lam. is of some local importance on Fisher Island, and supports a varied fauna consisting of *Cominella lineolata, Lepsithais vinosa, Hipponix conicus* (Schumacher), *Melanerita melanotragus, Micrastraea aurea* Jonas, *Serpulorbis sipho* (Lam.), *Fax tenuicostata* (Ten. Woods), *Sypharochiton maugeanus* and *Cryptoplax iredalei* (Ashby). The region where these mussels occur is sheltered from the waves, and has been occupied by mussels for a number of years.

Another change noted was the density of barnacle population. In 1954 there were not many barnacles on the island, but it was noted that there had been widespread and apparently successful spatfall in that year. This spatfall continued to survive, as is witnessed by the large number of *Chamaesipho* of uniform size on the shores of the island.

(4) *Blackman's Bay.*

A most interesting change has occurred in this area, where the limpets *Cellana solida* (Philippi) have become exceedingly rare or absent over much of the lower part of the Derwent estuary. In 1950, I described *Cellana* as occurring commonly at Blackman's Bay, especially on the platform at the northern end of the Bay. Examinations carried out in 1957 by myself and Dudgeon (*in litt.*) show that this limpet has become scarce over a considerable part of this coast. The reduction in the number of limpets has resulted in the virtual elimination of the Patelloid belt described earlier (Guiler, 1950). The band has been replaced by downward extension of the *Galeolaria* belt and partly by an upward extension of the *Austromytilus rostratus* belt.

Discussion.

The changes recorded above are all concerned with species which are known not to suffer large annual variations in population density. All of the species are of importance on the shore since they are concerned with the formation of belts of zonal significance. Some of the species, notably *Galeolaria, Pyura* and the mussels, are of even greater importance since they furnish an important habitat for other smaller species. Thus any major alteration in the numbers of these belt forming species will have an important effect on the shore as a whole. Not only may the zonation be changed but, if one of the habitat forming species is removed, the whole species composition of the shore may be drastically altered.

One of the features of the shores of southern Australia is the relative poverty of the fauna and flora of the upper parts of the tidal region, and that any changes in zonation thus will be noticed. The changes noted above were all observed on coasts which experienced a low tidal range of less than 5′ amplitude. Within such a narrow inter-tidal region any alteration in the belts is liable to be proportionately greater and liable to be noticed more easily than on a coast having a tidal range of 9′ or more. The absence of large growths of algae makes the observation of such changes easier.

The fact that the changes in the belts occur amongst those organisms which are found at or near Mean Sea Level (M.S.L.) may be significant. It was calculated (Guiler, 1950) that *Galeolaria* occurs at about M.S.L. and suffers from 18·71% air exposure. *Hormosira* and *Mytilus,* occurring lower on the shore than *Galeolaria,* would have a somewhat less exposure, with a maximum of 26% for *Mytilus.* In my 1950 paper, working on a semi exposed coast, I suggested that there exists a lethal level at about M.S.L. at which a large number of species "cut out." It was also noted that the level of M.S.L. varies from month to month. This variation is only slight, but it may be sufficient to furnish a very varying and critical habitat to those species that dwell at or near that level. This is shown by the fact that a number of zone forming and other species cut out at about that level.

The evidence provided by the Coles Bay observation points to there being intense interspecific competition at least between certain species at this level, namely *Hormosira* and *Galeolaria, Hormosira* and *Mytilus, Austromytilus* and *Hormosira,* while the Dodge's Ferry evidence shows that *Galeolaria* and *Pyura* and *Mytilus* are in a state of constant interspecific pressure, the absence of *Mytilus* enabling *Galeolaria* and *Pyura* to extend their vertical ranges. The limpet *Cellana* is dependent upon a smooth rock surface of sufficient area to permit the growth of algae and subsequent grazing by the limpet. Any encroachment upon their habitat by *Galeolaria* or barnacles will result in a restriction of the range of the limpet, and this is what happened at Blackman's Bay.

Southward and Crisp (1954) noted changes in the populations of British barnacles ascribing these changes to interspecific competition combined perhaps with other causes. Endean, Kenny and Stephenson (1956) record several instances where the zonation of the Queensland shores is controlled by interspecific competition. They found that *Pyura* overgrows *Galeolaria,* and that *Galeolaria* determines the lower limit of the barnacle zone.

Although interspecific competition is of great importance in determining the zonation, the conditions may be tipped in favour of one species or another by certain undetermined causes, as noted by Southward and Crisp. One feature of these changes is that only one species is immediately affected by them.

The thick masses of *Galeolaria* form in certain usually sheltered localities, and these aggregations apparently broke away from the substratum during the same year at widely scattered places on the Tasmanian coast, e.g., at Coles Bay, near the north-east, and Dodge's Ferry, in the south-east of the State. It may have been coincidence that this occurred at about the same time, but on the other hand it may well be part of a long-term cyclic change. It certainly was not due to a gale or gales. The immediate reason for the breakdown of the masses may be a mechanical breakdown of the tubes holding the mass to the substratum due to the excessive weight of the whole structure. This explanation may well be true of one group of *Galeolaria* tubes, but it can hardly suffice for hundreds of clusters breaking down at about the same time over at least 200 miles of coast. We can postulate a cycle or rhythm in *Galeolaria* with an initial high rate of larval settlement giving uniformly growing masses of *Galeolaria* tubes leading to tube clusters reaching a state of mechanical instability at the same time. All of the individual tubes in a *Galeolaria* aggregation are not of the same size, due to the settlement of subsequent larvae, but if this settlement rate is more or less the same over the whole coast then the breakdown will occur at the same time. This uniform rate of larval settlement is very difficult to concede, and at present I feel more inclined to ascribe the changes in *Galeolaria* population to some event or series of events, which may turn out to be cyclic in nature.

In the case of *Galeolaria,* some cause or causes led to the removal of the worm tubes from the rocks, and this created a biological vacuum on the shore. The surrounding unaffected organisms responded to this by a movement into the vacant area, as was also seen when *Mytilus planulatus* left a space on the shore at Dodge's Ferry. The rate of filling of the vacuum is not rapid, both where *Pyura* and *Mytilus* are the encroaching organisms.

However, the rate of recolonization by the zone forming species which had been removed may be very rapid. Experiments carried out on *Mytilus planulatus* beds at Blackman's Bay showed a very slow encroachment rate, but on removal of the whole mussel bed by a storm, the

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Plate 2.

Fig. 1. *Galeolaria* masses at Dodge's Ferry, December, 1949. The shore was thickly coated with masses such as this.

Fig. 2. The shore at Dodge's Ferry, March, 1956. Note the absence of *Galeolaria* masses and mussel beds. *Pyura* (dark masses on the seaward edge of the rocks) has spread and become a dominant species.

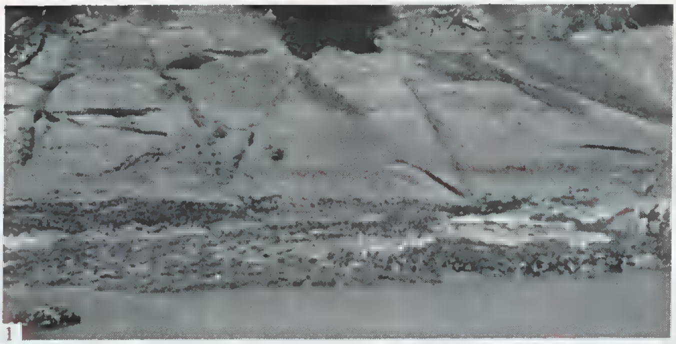

Plate 3.

Fig. 1. Honeymoon Beach, Freycinet Peninsula, January, 1950. Note absence of *Austromytilus*.

Fig. 2. The same, February, 1957. An *Austromytilus* belt is visible above the sea as an intermittent black band.

recolonization took a matter of weeks (Guiler, 1954). The association usually found with the mussels took very much longer, being dependent upon the growth of the mussels to a size sufficient to harbour the organisms of the endobiose.

To some extent, the fauna of the shore when considered as a whole may not alter much. If a *Galeolaria* association is removed and *Pyura* becomes more highly developed, certain of the organisms usually found with *Galeolaria* are often found under *Pyura*. However, this is not entirely true, and some animals disappear from the shore for as long as the association in which they occur.

Stephenson and Stephenson (1952, 1954) are strongly of the opinion that the basic zonal pattern will not change sufficiently to alter the whole pattern of zonation. Their conclusion can be applied to the coasts of Tasmania, where none of the alterations so far observed have done any more than slightly alter the zonation.

One important fact which has emerged from this long term project is that a collecting list made on one occasion may differ very greatly in its details from that made subsequently.

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